ADDITIONS TO "ANNOTATED KEY TO *PLATYNUS*"
(COLEOPTERA: CARABIDAE: AGONINI).

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Since publication of my "Annotated key to *Platynus*" (1973), I have discovered that two important entries were inadvertently dropped from early drafts and hence omitted in final proof.

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Page 192: replace discussion under entry for *P. consularis* and add entry for *P. convexulus*, as follows.

Platynus consularis is known only from various localities in the state of Guerrero. This species has been confused in collections and in the literature with *P. ebeninus* but is well distinguished by characteristics cited in the key, and the two species probably are not closely related.

Platynus convexulus (Casey), new combination.
   Anchomenus convexulus Casey 1920: 38. Holotype female (?), labelled "Tamaulipas Mex. . . ." (script), "TYPE USNM 47412" (USNM). Probably a female, but not sexed definitely since both front tarsi as well as all other claw bearing tarsal articles are lost.
   Agonum convexulum, Csiki 1931: 862 (subgenus *Anchomenus*); Blackwelder 1944: 41.
   This form is evidently quite closely related to *P. porrectus*, and perhaps is conspecific with it. Specimens seen from the state of Hidalgo agree with the holotype of *P. convexulus*. Specimens from various localities in the Trans-Volcanic Sierra differ by having dorsoapical setae on the hind femora, and may represent a distinct species.

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Page 212: insert following between entries for *P. teter* and *P. tlamayensis*.

Platynus tinctipennis (Bates), new combination.
   Colpodes tinctipennis Bates 1891: 257. Lectotype female, here designated, labelled "TYPE H. T.", "Ciudad, Durango. Höge." (BMNH).
   Colpodes tinctipennis, Csiki 1931: 764; Blackwelder 1944: 40.
   This species is known only from the original localities in Durango, Ciudad and Refugio.

REFERENCE

Whitehead, D. R. 1973. Annotated key to *Platynus*, including *Mexisphodrus* and most *"Colpodes"*, so far described from North America including Mexico (Coleoptera: Carabidae: Agonini). Quaestiones Entomologicae 9: 173-217.

THE EVOLUTION OF THE INSECT HEAD:
THE ENDLESS DISPUTE*

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> It would be too bad if the question of head segmentation ever should be
> finally settled; it has been for so long such fertile ground for theorizing
> that arthropodists would miss it as a field for mental exercise.
>   Snodgrass, 1960

Head segmentation in insects has long been a subject of dispute. The controversy concerns possible pregnathal segments, namely intercalary, antennal and preantennal, and the presence or absence of an acron. The total number of segments has been placed as low as three and as high as seven as seen in a brief review of the theories by Snodgrass, DuPorte, Butt, Ferris, Sharov, Roonwal, Chaudonneret, Matsuda, Imms and Manton, Eastham, Tiegs and Weber, Scholl, Rempel and Church. In the embryo of Lytta viridana *(Coleoptera: Meloidae) an intercalary segment is recognized by the presence of coelomic sacs, a neuromere (tritocerebrum), and apodemes (anterior tentorial arm); an antennal segment by a pair of appendages (antennae), coelomic sacs, a neuromere (deutocerebrum), and apodemes (mandibular extensor apodemes); a preantennal segment by a pair of appendages (labrum), coelomic sacs, and apodemes. The proposal is made that the ancestor of the insect was annelid-like, that the prostomium became the acron and that the six originally postoral segments joined the acron to form the head tagma. The theory differs from the classical theory of a six-segmented insect head in that the labrum is considered to be appendiculate innervated originally by the nervus connectivus from a preantennal neuromere (prosocerebrum).*

La segmentation de la tête des insectes a été depuis longtemps le sujet d'une longue dispute. Le problème concerne les segments préoraux: l'intercalaire, l'antennaire et le préantennaire, et la présence ou l'absence d'un acron. Le nombre de segments varie entre trois et sept selon les courtes revues de ces théories par Snodgrass, DuPorte, Butt, Ferris, Sharov, Roonwal, Chaudonneret, Matsuda, Imms et Manton, Eastham, Tiegs et Weber, Scholl, Rempel et Church. Chez l'embryo de Lytta viridana *(Coleoptère: Meloidae) un segment intercallaire est reconnu par la présence de sacs coelomiques, d'un neuromère (tritocérébrum) et d'apodèmes (embranchement antérieure, du tentorium); un segment antennaire est reconnu par la présence d'une paire d'appendices (antennes), de sacs coelomiques, d'un neuromère (deutocérébrum) et d'apodèmes (apodèmes des extenseurs des mandibules); un segment préantennaire est reconnu par la présence d'une pair d'appendices (labre), de sacs coelomiques et d'apodèmes. Nous proposons que l'ancêtre des insectes ressemblaient les annelides, que le prostomium est devenu l'acron et que les six segments postoraux originaux ont joint l'acron pour former la tête. Cette théorie diffère de la théorie classique de la tête de l'insecte composée de six segments en ce que le labre est considéré comme innervé par le* nervus connectivus *d'un nuromère preantennaire (prosocérébrum).*

INTRODUCTION

The problem of head segmentation in insects has been a lively topic of discussion since the turn of the last century. Numerous papers have appeared since then, each one outlining, often at great length, the history of evolutionary thought with respect to head segmentation. One of the latest and most detailed reviews is given by Matsuda (1965). When the latter work appeared in print it seemed that the problem was largely solved and little would be gained in reopening the debate. But new information has been published lately which suggests that part of the protocerebrum is a preantennal neuromere (Malzacher, 1968; Scholl, 1969) and that the labrum, which has been the center of the controversy, is indeed an appendicular structure (Rempel and Church, 1971).

Of further significance is that recent publications still feature the theories expounded by North American workers, notably Snodgrass, Ferris and Butt, although the weight of evidence is against these theories. Of concern is the adoption of the Snodgrass (1935) theory by the author of a monumental work on the structure and function in the nervous systems of invertebrates (Horridge, 1965) and by the author of a recent textbook in entomology (Romoser, 1973). The Ferris (1950) theory which has never received serious consideration was featured by Demerec (1950), in his "Biology of *Drosophila*". Two recent papers (Steinmann, 1970; Dixit, 1972) follow Butt (1957, 1960) in assigning the labrum to the intercalary or tritocerebral segment and are thus subject to the same criticism as the papers by Butt.

THE INSECT HEAD

The Problem of Head Metamerism in Insects

In the study of animal evolution various approaches have been used. The most direct evidence is afforded by the fossil record, but in the case of insects, palaeontology has not given us the information that we require. The secret of head metamerism should be looked for in early Devonian fossils for the primitive insect stock appeared in the Devonian (Smart and Hughes, 1972), but such material is not available. Indeed, we even lack sufficient later palaeontological specimens to enable us to reconstruct an undisputed phylogenetic tree for the insectan world (Scudder, 1973).

Similarly, problems have been encountered in studies of comparative morphology. First, most insect morphologists who have been concerned with head segmentation assume that the present day arthropods are the product of a monophyletic line of evolution. On this assumption any theory of head segmentation for insects must be equally applicable to the Chelicerata and the Crustacea. That this approach is questionable is evident from the extensive studies of Tiegs and Manton (1958) and Manton (1964). These authors advance evidence that in the case of arthropods we are confronted with a di- or polyphyletic origin. For example, Manton has shown that the mandibles have evolved independently in (i) the Crustacea; (ii) the Chelicerata; (iii) the Onychophora, Myriapoda, Insecta. In the last the mandible is a modified whole limb, while in the first two the jaw arises from a part of the limb.

Of additional significance is the arrangement of cephalic apodemes. The Crustacea possess no common basic plan, while in the myriapods and hexapods the apodemes are arranged in an intersegmental series that is similar in the two groups — although the posterior tentorial arm is absent in the myriapods. On this thesis the relationship between Crustacea and Insecta is a distant one. For this reason I believe that study of evolution of the arthropod head should be done independently in the three major groups in the hope that such studies will indicate the extent of phylogenetic relationships or the extent of convergent evolution.

A second difficulty from studies of comparative morphology arises from the fact that these studies are often based on structural features of the adult. Bearing in mind the great morphological changes that many insects undergo in their ontogeny, such studies seem to be doomed from

the beginning. It is a study of a 'finished' product and this should make it suspect. Morphologists now generally agree that sutures in the larva and adult with the possible exception of the postoccipital suture cannot be used in determining segmental boundaries (Chapman, 1969). Further, in morphological studies too much emphasis has been placed on muscle arrangement and muscle innervation. Muscles may be composite structures derived from more than one mesodermal somite, and muscles can also traverse two or more segments before reaching insertion. Some authors have emphasized muscle innervation in head segmentation, but motor neurons do not invariably innervate muscles of their own segment and sensory neurons do not invariably lead to the ganglion of their own segment. The above statement is based on the findings of Horridge (1965) who has made an unusually detailed study of the nervous system of invertebrates.

Because of the inadequate fossil record and the inadequacy of the morphological approach in studies of head segmentation, I agree with Matsuda (1965) that "a concept of the constitution of the insect head should be based primarily on embryological data". My views are based mainly on studies of the embryonic development of *Lytta viridana*, a blister beetle. Behavioral and physiological studies of this species were first undertaken by Dr. Norman Church, then a member of the Federal Department of Agriculture at Lethbridge, Alberta. Later he continued this work at Saskatoon and collaborated with me in the developmental studies.

The term segment is treated here in terms of a *metamere* which is defined by Snodgrass (1935) as a body division of the embryo; an embryonic somite or primary body segment. This definition is quite insufficient for our purpose. In defining a metamere four criteria are now generally used, namely: the presence of a pair of mesodermal somites; a pair of appendages; a pair of apodemes, and a neuromere. It must be understood that during the long period of evolution a component may be greatly reduced or even be lost. A controversy has arisen over the relative importance of the different components. Some authors have emphasized coelomic sacs, while others have minimized them. Some have stressed innervation and muscle arrangement. But the chief difficulty has arisen because of the frequent neglect of embryological studies.

The controversy in regard to head segmentation in arthropods concerns exclusively possible pregnathal segments, namely intercalary, antennal, and preantennal. There has never been any disagreement with regard to the status of the mandibular, maxillary, and labial segments. The total number of segments has been placed as low as three (with no pregnathal segments) and as high as seven. There has also been disagreement regarding the presence or absence of an acron (= prostomium).

A brief review of the theories that have been proposed from time to time will now be given. The selection was made to demonstrate the extent of difference in thought. Detailed accounts of the history of evolutionary thought regarding head segmentation are extant and readily available (Matsuda, 1965).

Theories of Head Segmentation

The Snodgrass Theory (Fig. 1). — Robert Evans Snodgrass was one of the world's leading insect morphologists and anatomists, a very productive researcher, a prominent teacher, an artist and philosopher. He had a colorful and eventful career. For nearly a quarter of a century he held a dual post in the Federal Bureau of Entomology and lecturer in entomology at the University of Maryland (Mallis, 1971).

A biographer (Thurman, 1959) has this to say of Snodgrass. He was a "dignified, erect, gracious unassuming gentleman...". A man with "a phenomenal memory for facts and events, a wealth of basic knowledge at his ready command, thorough training in the use of the Classical and Romance languages, and an unlimited vocabulary in English and German...".

Snodgrass (1935, 1960) adopted the theory originally proposed by two European workers, Holmgren (1916) and Hanström (1928). In accordance with this theory the insect head consists of an acron and four metameres. The acron is large and encompasses the ocular, labral, and antennal regions. The labrum is believed to be a mere outgrowth over the stomodaeum. It is not appendiculate and there is no labral segment. The presence of labral coelomic sacs recorded in some forms is not believed to indicate a segment. The antennae are not homologous with other appendages, and the deutocerebrum is not a separate ganglion but with the protocerebrum constitutes the primitive brain, the archicerebrum.

The theory has had widespread acceptance in North America, but it has been criticized by European workers, notably Manton (1949) and Siewing (1963) and others. Although generally considered to be the leading North American insect morphologist, Snodgrass repeatedly betrayed unfamiliarity with insect embryology. Thus he assigned the origin of segmentation phylogenetically to the ectoderm when developmental studies have clearly shown that the mesoderm segments *before* the ectoderm and thus sets the pattern of segmentation. His claim that coelomic sacs of the acronal region (as defined by him) are best developed in higher arthropods is contradicted by embryology. Thus some coleopteran embryos have well developed coelomic sacs in the head (Ullmann, 1964; Rempel and Church, 1969; Church and Rempel, 1971), while they are totally absent from dipteran embryos. His denial of appendiculate status to the antennae must be rejected by every modern insect embryologist. The antennae arise in the embryo as appendage-like outgrowths; they are provided with large coelomic sacs, apodemal invaginations are present and the deutocerebrum is the neuromere. Although many workers in the past, following Snodgrass, have denied segmental status to the labrum, recent studies provide ample evidence that the labrum represents the fused appendages of a labral segment (see below).

The DuPorte Theory (Fig. 2). — Dr. Ernest Melville DuPorte rightfully deserves the title Dean of Canadian entomology. But his reputation flows beyond the border of this country and we can refer to him as one of North America's leading insect morphologists and teachers of entomology. Dr. DuPorte was born in the West Indies in 1891 and in 1910 came to Canada to enrol in entomology at McGill University. Upon receiving the Ph.D. he joined the faculty of McGill and served that institution with great distinction until his retirement in 1957. At the time of his retirement it was said that half of Canada's practicing entomologists had at one time or another studied under Dr. DuPorte. On a more personal basis one might say that this outstanding researcher and teacher is noted for the warmth of his personality and fondness for his students. It is no wonder that he enjoys the high esteem and affection of all. Dr. DuPorte, now in his 80's, is presently completing a textbook on insect morphology. One might well ask "Why has there not appeared ere now an extended biography of this outstanding Canadian biologist?"

The DuPorte theory is an extension of the Snodgrass theory and suffers from the same weakness. Embryological evidence is underrated and coelomic sacs are not regarded as a valid criterion of metamerism. The acron is large bearing the eyes, the antennae and the labrum. That is, the preoral region is entirely unsegmented. Like Ferris he does not recognize an intercalary segment. But embryological evidence contradicts DuPorte's theory. The presence of an intercalary and antennal segment has been established beyond doubt by a wealth of developmental studies.

The Butt Theory (Fig. 3). — Dr. F. H. Butt was for many years Professor of Insect Morphology and Embryology at Cornell University. He is co-author (with O. A. Johannsen) of the Textbook of Embryology of Insects and Myriapods. Dr. Butt, now retired at Friday Harbor on the Pacific, was for many years interested in the segmentation of the insect head and published several papers on the subject. With Snodgrass he identified the acron as the region that bears the compound

eyes and the antennae, but excludes the labrum. The latter is looked upon as the fused labral appendages, and since the labrum is innervated from the tritocerebrum, it is considered to be part of the premandibular or intercalary segment. The antennae are not considered to be appendicular and the deutocerebrum is not a segmental ganglion but with the protocerebrum corresponds to the archicerebrum of the annelid ancestors. The theory has been criticized by Snodgrass (1960) on the ground that the labral nerve is largely if not entirely a sensory nerve and thus cannot be used in determining segmentation. The theory has also received strong criticism by Manton (1960), a criticism which I believe to be intemperate. To settle the dispute we need further detailed studies of the nerve pathways in the labral nerve and the nervus connectivus.

The Ferris Theory (Fig. 4). — Gordon Floyd Ferris was born in Kansas in 1893. Early in his life he moved west and was for nearly a half a century associated with Stanford University, first as a student 1912-1917, and then as a faculty member 1917-1958. As professor he had a distinguished career (Mallis, 1971). According to one biographer he was one of the giants of taxonomic entomology in this century and this is borne out by his publications which number 217. He was also an accomplished teacher of entomology and a field naturalist. Ferris was an independent and forceful personality; he stated what was on his mind in energetic language. Students held him in awe, but were attracted to him and inspired by him. They came from various states outside California and from foreign lands. But in a university an overpowering force can exert a negative influence. And so it was with Ferris. The publications of many of his students betray too strong a Ferris stamp.

Ferris' theory of head segmentation is most unusual. It is based on two main assumptions, namely that the principal transverse sutures of the adult are intersegmental lines marking the limits of the labral, clypeal, oculo-antennal, mandibular, maxillary, and labial segments, and that a ganglion innervates a segment to which it originally belonged. The theory is based largely on the findings of one of his co-workers, Miss Henry. Since the theory is based largely on innervation, a difficulty is encountered in that the labrum is innervated from the tritocerebrum. A ready explanation is found by assuming that the tritocerebral ganglion has phylogenetically been shifted posteriorly. There is no room for the intercalary segment which Ferris claims was 'invented'. A weakness of the theory is that it is based on features of the adult insect; on the belief that the nervous system can be used to determine homology although no attempt is made to trace nerve pathways. But the greatest drawback is the total disregard of embryological evidence. The theory is now merely a historical curiosity that has no further place in the entomological literature.

. *The Sharov Theory* (Fig. 5). — One of the leading Russian authorities to take part in the controversy of head segmentation was A. G. Sharov. A brief outline of his biography indicates a remarkable career. He was born near Moscow in 1922. At the age of 17 he entered the University of Moscow, but his education was interrupted by the war. Upon graduation in 1950 he joined the Institute of Animal Morphology and later transferred to the Paleontological Institute, Academy of Sciences. Here he rose quickly from instructor to senior scientist. He was the leader of a series of expeditions to Asiatic Russia to collect vertebrate and invertebrate fossils. As a scientist he was very productive and in his short life published 67 scientific papers and monographs. Of added interest is that he appeared to have complete mastery of English.

Sharov believes in the monophyletic origin of the arthropods and therefore maintains that a theory of head segmentation must fit the entire phylum. He postulates a seven-segmented head. The first or anteriormost segment is the labral, and the labrum is appendiculate. This is followed by the ocular or preantennal segment. The compound eyes are considered to be modified limbs. Then follow the segments in the usual way. Sharov's book *Basic Arthropodan Stock* in which he outlines his theory has been severely criticized by Hedgpeth (1967) who calls the

book an "unnecessary and misleading contribution."

The Roonwal Theory (Fig. 6). – M. L. Roonwal published his theory of head segmentation in 1938. He postulates a seven segmented insect head. The acron, and with it the archicerebrum, has disappeared. The first segment is the labral and its neuromere is part of the protocerebrum. It is followed by the preantennal, with a second part of the protocerebrum as the neuromere. The protocerebum is thus composed of two pairs of ganglia. Then follow in succession the antennal, intercalary, mandibular, maxillary and labial. Roonwal is aware that the labrum is innervated from the tritocerebrum and not from the protocerebrum, but considers this to be a secondary feature. He thus seems to anticipate the view expressed later by Scholl (1969).

The Chaudonneret Theory (Fig. 7). – Jean Chaudonneret is a morphologist and embryologist of note. He was born in Dijon, France and received his education at the Universities of Dijon and Paris. He has been associated with the University of Dijon since 1943. His publications consist of a series of papers dealing with the morphology and embryology of the insect head and the gnathal region of the Malacostraca.

According to Chaudonneret (1966) the acron is small, well hidden. The first segment is the protocephalic or preantennal bearing the eyes. This is followed in succession by the antennal, tritocerebral, superlingual, mandibular, maxillary and labial. The uniqueness of this theory is the presence of the superlingual segment, the superlinguae being considered appendicular. The labrum is composite in structure derived from several originally postoral segments. The acron is overgrown by parts of these segments. Matsuda (1965) points out the weakness of this theory in that the superlinguae cannot be appendages of a separate segment for according to Silvestri (1933) they arise embryologically from the posterior region of the mandibular segment and the anterior region of the maxillary segment. Moreover, since Chaudonneret's theory is based mainly on a study of *Thermobia*, it is of interest to note that Larink (1970) found no evidence for the presence of a superlingual segment in the embryonic development of *Lepisma*.

The Matsuda Theory (Fig. 8). – Dr. Matsuda studied at Stanford under Ferris. He is presently associated with the Federal Department of Agriculture in Ottawa. On the basis of his excellent publications in insect morphology, we must look upon Dr. Matsuda as one of the leading insect morphologists on this continent.

Dr. Matsuda's (1965) theory of head segmentation is outlined in his book the "Morphology and Evolution of the Insect Head". I briefly summarize his views. The acron is large and bears the eyes and labrum. The neuromere is the protocerebrum. There is no preantennal segment and the bilobed labrum is not appendicular. The first definitive segment in insects is the antennal, with the deutocerebrum as it neuromere. The antennae are appendicular. The head is thus made up of an acron and five segments.

The Imms-Manton Theory (Fig. 9). – Angustus Daniel Imms is one of the best known English entomologists. His fame rests largely on his widely used General Textbook of Entomology and he must be looked upon as being first and foremost a teacher, rather than a researcher. There is no photograph of Imms in existence, but a sketch by an artist is in the possession of Sir Vincent Wigglesworth who very kindly sent me a copy and a biography of Imms.

Imms was born in 1880. He received his early education, which was frequently interrupted by ill health, in Birmingham. In 1903 he graduated from London and two years later entered Cambridge as an 1851 Exhibition Science scholar. At Cambridge he came in contact with some of the best entomologists of the day. He graduated in 1907 with a B.A. degree and was awarded the Darwin Prize of Christ's College. In the same year Birmingham bestowed upon him the D.Sc.

After graduation Imms spent six years in India, first as professor of biology at the University of Allahabad and later as Forest Entomologist of the Government of India. For reasons

of health he returned to England and accepted a readership in Agricultural Entomology at Manchester. During the war years 1914-1918 he tried repeatedly to enlist but was rejected on account of ill health. In 1918 Imms moved to the Experimental Station at Rothamsted and remained there until 1931. While at Rothamsted he wrote the General Textbook of Entomology, the book being published in 1925. This immediately brought him widespread recognition at home and abroad. He travelled widely and in 1925 and again in 1928 made extensive tours in Canada and the United States. In 1929 he was elected a Fellow of the Royal Society, and in 1931 accepted a readership in entomology at Cambridge. Here he established a fine record as a teacher, but he also 'produced some valuable memoirs bearing particularly on morphological problems fundamental to questions of the ancestry of insects and phylogenetic relationships of the main orders' (Thorpe, 1949). His theory of head segmentation in insects appears in his textbook and I shall briefly outline his views as found in the 1957 revised edition. But we must first introduce another British authority whose views are in close agreement with those of Imms.

Sidnie M. Manton, the holder of an impressive list of degrees and honours:

> M.A., Ph.C., Sc. D. (Cambridge)
> Fellow, Royal Society of London
> Hon. Doctor Filosophie (Univ. Lund)
> Fellow, Linnean Society
> Linnean Gold Medalist.

The above academic achievements speak clearly of a scientist and scholar of a high order. Academically Dr. Manton has been associated with Kings College, with Queen Mary College, and the British Museum of Natural History. She has to her credit numerous publications dealing with the morphology, embryology and evolution of the Arthropoda, especially Crustacea and Onychophora. She has an incisive mind, a great background of knowledge and a great facility in writing. As a consequence the word 'monumental' can very well be ascribed to her work. But she can be intolerant of the views of others and I believe it is in order to call to Dr. Manton's attention the words of the philosopher Sir Thomas Browne, written in his *Religio Medici* some three centuries ago:

> "I should never divide myself from any man upon the difference
> of an opinion or be angry with his judgement for not agreeing
> with me."

Imms accepts the classical theory of head segmentation and recognizes an acron and six metameres: preantennary, antennary, intercalary, mandibular, maxillary, and labial. He associates the preantennary segment with the protocerebrum although the latter may also comprise the archicerebrum or primitive prostomial ganglion. The labrum is simply an unpaired sclerite overhanging the mouth. It is not appendiculate, and there is no labral segment.

Manton's views are in close accord with those of Imms, and we need not elaborate further.

The Eastham Theory (Fig. 10). — Dr. Eastham is associated with the Department of Zoology, Cambridge University. His theory is based on a detailed study of the embryology of *Pieris rapae*, the cabbage butterfly, published in 1930.

In the early embryo Eastham made the important observation that there are six pairs of appendages in the regions that ultimately form the head tagma. The first pair fuse early and develop into the labrum; the second pair are large and become the antennae; the third pair are rudimentary. The fourth, fifth and sixth pairs form the mandibles, the maxillae and labium respectively. Of special significance are the following. The labrum arises as two appendages and each is provided with a somite. The protocerebrum is considered to be the neuromere. Of interest too are the rudimentary appendages of the tritocerebral segment. Their presence clearly indicates that the labrum cannot be the appendage of this segment. According to

Eastham then, the insect head is made up of six segments, which is in agreement with the classical theory of head segmentation. It differs from the view of others in that he omits the acron. The ocular region is thus part of the labral segment. Eastham must be accorded the credit for calling attention to the importance of the cephalic apodemes as an indicator of the segmental constitution of the embryonic head.

The Tiegs and Weber Theory (Fig. 11). — In November 1956 the entomological world lost two of its most illustrious members. The first was Oscar Werner Tiegs. The second was Hermann Weber. Tiegs was born in Brisbane, Australia, on March 12, 1897. His parents were of German origin and had migrated to Australia at an early age. When still quite young he showed a great interest in insects which seemed to foreshadow the remarkable contribution he was later to make in entomology. Educated at the University of Queensland and Adelaide University he joined the faculty of the University of Melbourne in 1925 and served that institution until his death.

Tiegs' early work involved the study of striated muscle in both vertebrates and invertebrates, and in these studies he was far ahead of his times. One wonders what this man would have achieved had he been able to draw on modern knowledge of biochemistry and had he had at his disposal modern equipment. In the field of entomology he made truly outstanding contributions in the embryology and phylogeny of the Myriapoda and Insecta. These studies were undertaken in the hope that they would throw light on the evolution and structural relationships of the Arthropoda. His work is characterized by attention to minute detail which gives it lasting value. He achieved international acclaim, especially in Britain where formal recognition of his work was to be accorded him at the Darwin celebrations in 1958. He died unfortunately in 1956 at the age of 59.

Herman Weber was the 'pride' of German entomology and zoology. But his fame extended far beyond the borders of his homeland, and other countries vied with each other to honour this illustrious man. His outstanding scientific achievements were recognized by academicians in German universities generally and there was keen competition for his services — Bonn, Danzig, Freiburg, Münster, Vienna, Strassburg, Tübingen. During the war he suffered internment and this seriously undermined his health which cut short his career at the age of 57. Weber made brilliant contributions in three spheres. He was the author of numerous outstanding scientific papers; he was involved in the editorship of prestigious scientific journals such as *Zoologische Jahrbücher, Fortschritte der Zoologie* and others; he was the author of several textbooks. His *Lehrbuch der Entomologie* was written in one year and it is now regarded as a rare jewel in zoological literature. I consider his *Grundriss der Insektenkunde* written in 1938 still as the finest textbook of entomology. Unfortunately to Canadian students with knowledge limited to English or French it is a closed treasure.

Tiegs' (1941, 1947) theory of head segmentation is based largely on his detailed studies of the embryology of Symphyla and Pauropoda. Weber (1952) made a lengthly review of the various theories of head segmentation and his views largely coincide with those of Tiegs. We may summarize these as follows:

The acron is homologous with the annelid prostomium. It bears the archicerebrum which originally was made up of a small median unpaired nervous element. To this were later added a pair of ganglia which form the larger part of the archicerebrum and innervate the eyes. The acron is followed by 6 segments. The first is the preantennal segment, or prosocephalon. Its neuromere is the prosocerebrum (Nebenlappen; Accessory Lobe). It is closely associated with the archicerebrum to form what is commonly called the protocerebrum. The second metamere is the antennal. Its appendages, the antennae, are innervated by the deutocerebrum. This is followed by the premandibular or intercalary segment with the tritocerebrum as its neuromere. The labrum, according to this theory, is composite in structure and is the product of the three

preoral segments. ~~There is thus no labral segment~~. The statement is significant in view of what many other researchers believe.

In 1963 Rolf Siewing of the Zoological Institute of the Christian-Albrechts University at Kiel made an extensive analysis of the problem of head segmentation in arthropods based on a review of the literature. His conclusions are in rather close agreement with those of Tiegs and Weber. He too concludes that there is an acron and six metameres, namely: preantennal, antennal, premandibular, mandibular, maxillary and labial. The labrum is considered to be solely part of the preantennal segment but he is not prepared to assign it appendiculate status.

The Scholl, Rempel and Church Theory (Fig. 12). — During the last few years Dr. Church and I have made a rather detailed study of the embryonic development of *Lytta viridana*. Our studies completely confirm the findings of Tiegs, Weber and Siewing. But we go a step further. We find that the labrum must be considered appendiculate. We conclude that the insect head consists of the annelid prostomium (referred to as the acron) and six metameres, the anterior-most three having assumed a preoral position.

I now want to outline the proof for our theory. May I point out again that there has never been any disagreement regarding the status of the mandibular, maxillary and labial segments. I therefore limit the discussion to the status of the premandibular or intercalary segment, the antennal segment, and the preantennal or labral segment.

First the intercalary segment. Its existence has been denied by only two workers, DuPorte and Ferris. Ferris called the segment an 'invention'. What does embryology show? In 60 h embryos of *Lytta*, parasagittal section (Fig. 14), the intercalary segment is as distinct as the succeeding segments. Note the coelomic sac. At 70 h (Fig. 15) a neuromere (tritocerebrum) is formed; at 80 h (Fig. 16) the apodemal invagination (the anterior tentorial arm) is prominent. At this stage the tritocerebrum has joined the brain. Eastham (1930) (Fig. 13) recorded rudimentary premandibular appendages. Thus the four criteria of a metamere are met.

What about the antennal segment? Here the North American workers (Snodgrass, Ferris, DuPorte and Butt) are in a separate class from the European workers in that they reject appendiculate status for the antennae and deny the presence of an antennal segment. Let us recall that we have four criteria for a segment. In an early embryo, a whole mount with all embryonic membranes removed, appendage-like outgrowths are found from the labral to the first abdominal segment (Fig. 13). Note that the largest among them are the antennae. In other words, the latter arise like all other appendages. The statement has been made that the antennae in structure differ markedly from the other appendages. In reply we may point to the great plasticity of the arthropod appendage. It can be changed in various ways. For example, in *Lytta* the appendages of the first abdominal segment change into glands, the pleuropodia. That antennae generally have large coelomic sacs is well known from embryology (Fig. 16). That satisfies two criteria. Antennal apodemes have been reported by a number of workers. We observed them in an early embryo of *Lytta* (Rempel and Church, 1971, Figs. 2, 7, 8). In this species, these apodemes extend backward into the mandible (Fig. 18). As the latter rotate in a posteromedian direction through an angle of 120° (Fig. 19), the apodemes become located at the outer edge of the mandible and later serve as support for the mandibular extensor muscles. Our view of the ultimate fate of the antennal apodeme differs from that of Scholl (1969) who maintains that it forms the dorsal arm of the tentorium.

That leaves us the problem of an antennal neuromere. The four leading American workers mentioned above believe that the archicerebrum, the ancient brain, divided secondarily into protocerebral and deutocerebral lobes. In other words, according to them the deutocerebrum is not a segmental ganglion. This view is rejected by modern embryologists, for it is well known that the deutocerebrum arises in the embryo apart from the protocerebrum. In the illustrations (Figs. 20 and 21) the deutocerebrum with the sensory and motor neurons of the antennae are

indicated.

That brings us to the final, the central problem, the crucial point of the long-lasting controversy. With few exceptions the entomologists of the world who have concerned themselves with head segmentation look upon the labrum as merely an outgrowth of the body wall in front of the stomodaeum. The view is well expressed by Snodgrass (1960) when he says, "it seems much simpler to accept the labrum for what it appears to be in all arthropods from trilobites to insects, namely, a preoral lobe of the head". But you will recall that when I discussed theories of head segmentation that Eastham as early as 1930 considered the labrum the fused labral appendages and the protocerebrum their neuromere. Butt in 1957 and again in 1960 advanced the theory that the labrum resulted from the fused appendages of the intercalary segment. Siewing in 1963 accepted the presence of a preantennal or labral segment but was not prepared to assign appendiculate status to the labrum. There are numerous references in the literature to the early appearance of the labrum as two appendage-like outgrowths. This is especially well seen in *Pieris* (Fig. 13), in *Tenebrio* (Ullmann, 1964) and in *Lytta* (Rempel and Church, 1969). That each appendage may have a somite laid down *in situ* is well documented. In 1969 Scholl made a detailed study of the embryonic development of the head of the stick insect. He set out to investigate first whether there is a distinct region between the acron and the antennal segment which can be demarcated from the two, and which has not been translated there secondarily, and, second, whether one can assign segmental status to this area. On the bases of the development of the mesoderm Scholl could delimit three preoral regions: labral, antennal and premandibular. He is inclined to look upon the labrum as an appendicular structure.

Reference has been made to the intersegmental arrangement of cephalic apodemes. In 1965 Matsuda made a careful survey of the literature in regard to cephalic apodemes. His findings are summarized in Fig. 17. According to Matsuda no one had ever found apodemes in association with the labrum. But in 1971 we discovered these apodemes in early *Lytta* embryos (Figs. 18, 19). Also Scholl (1969) lists the following cephalic apodemes: labral (Frontalleisten?), antennal, intercalary, mandibular, maxillary and labial. Scholl believes that the arrangement of the apodemes can be used as a criterion for head segmentation if used in association with other criteria.

This leaves us the last hurdle. If there is a labral segment, what is its neuromere and what is its innervation? If the labral segment is a preantennal segment, then we must look for its neuromere in front of the deutocerebrum and for a nerve that leads from here to the clypeolabral muscles. According to Scholl (1969) the corpora pedunculata and the optic centres are common to the Annelida and Arthropoda. But the central body and the protocerebral bridge are found in arthropods only. Hence we may look upon the optic centres and the corpora pedunculata as the archicerebrum. The rest of the protocerebrum may then represent the preantennal neuromere, or the prosocerebrum. This is in agreement with the view of Larink (1970) and the view of Malzacher (1968) who lists the following sequence:

> Archicerebrum — Optic ganglia
> > corpora pedunculata
> Preantennal neuromere — Neurosecretory cells of the pars intercerebralis
> > Protocerebral bridge
> > Central body
> > Accessory lobe (Nebenlappen)
> Antennal neuromere — Deutocerebrum
> Intercalary neuromere — Tritocerebrum

I have illustrated this diagrammatically in Fig. 20.

In many orders of the Hemimetabola innervation of the clypeolabral muscles is via the

nervus connectivus, the frontal ganglion, and the nervus procurrens. Scholl (1969) believes that this was the original mode of innervation and that innervation via the labral nerve is a secondary acquisition. I have illustrated this in Fig. 21.

I now want to summarize my argument. The ancestors of the insects were annelid-like. The prostomium housed the archicerebrum, or primitive brain. All other ganglia were postoral (Fig. 22). The next forward step involved the acquisition of a haemocoel, a cuticle, segmental appendages, and apodemes for improved muscle attachment (Fig. 23). Over a period of millions of years cephalization involved a progressive shift of ganglia forward into a preoral position. The first one to join the archicerebrum was the labral (Fig. 24). While the archicerebrum began to shift dorsad and caudad, the labrum (a pair of fused appendages) shifted caudad to form a preoral cavity. We observe this phenomenon today in embryonic development. The labral nerve is the nervus connectivus. The next ganglion to shift into a preoral position is the antennal (Fig. 25). Finally the tritocerebral ganglion did phylogenetically what it does today ontogenetically. It too shifts from a postoral into a preoral position. The mandibular, maxillary and labial ganglia move forward, fuse, but retain their postoral position. The insect head thus consists of an acron and six metameres (Fig. 26). The appendages of the first metamere fuse to form the labrum; the appendages of the second become the antennae; those of the third are lost, although occasionally present in the early embryo. The appendages of the fourth, fifth and sixth segments develop into the mandibles, maxillae and labium respectively.

The theory proposed here is in line with the classical theory of a six-segmented insect head, and I believe it is in close agreement with the facts as we know them today.

ACKNOWLEDGEMENTS

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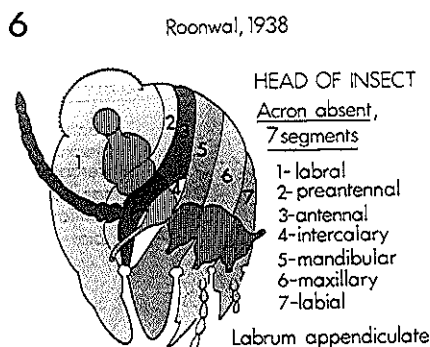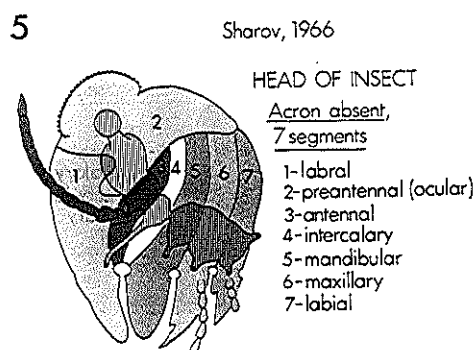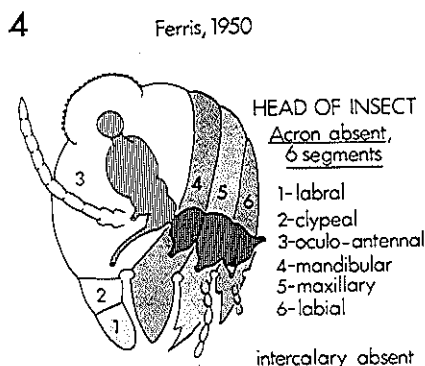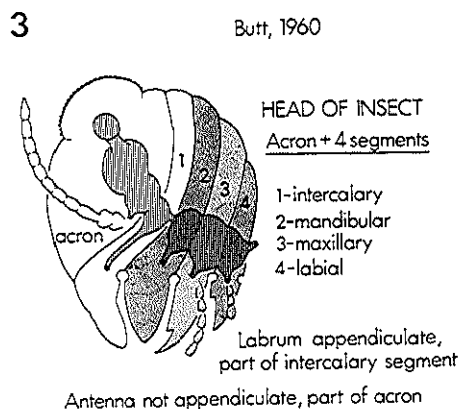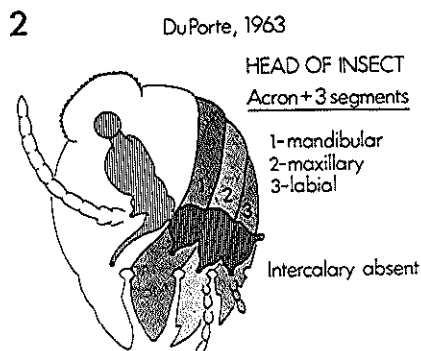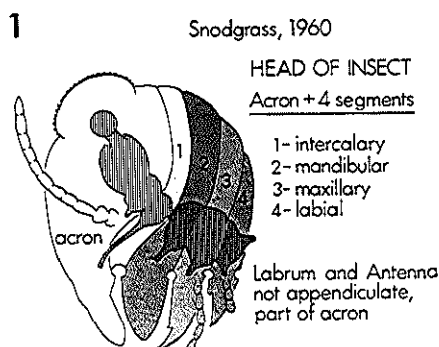
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FIGURE LEGENDS

Fig. 1.   The theory of Head Segmentation by Snodgrass.
Fig. 2.   The DuPorte Theory.
Fig. 3.   The Butt Theory.
Fig. 4.   The Ferris Theory.
Fig. 5.   The Sharov Theory.
Fig. 6.   The Roonwal Theory.
Fig. 7.   The Chaudonneret Theory.
Fig. 8.   The Matsuda Theory.
Fig. 9.   The Imms-Manton Theory.
Fig. 10.   The Eastham Theory.
Fig. 11.   The Tiegs-Weber Theory.
Fig. 12.   The Scholl-Rempel-Church Theory.
Fig. 13.   The embryo to show appendages and somites. Redrawn from Eastham, 1930, modified.
Fig. 14.   Parasagittal section of 60h embryo of *Lytta viridana* to show coelomic sacs. Note
           intercalary segment.
Fig. 15.   Parasagittal section of 70h embryo to show formation of ganglia. Note tritocerebral
           ganglion.
Fig. 16.   Parasagittal section of 80h embryo. Note: tritocerebrum as part of the brain; antennal
           coelomic sac; intercalary apodeme or anterior tentorial arm; maxillary apodeme or
           posterior tentorial arm; suboesophageal ganglion.
Fig. 17.   Hypothetical arrangement of cephalic apodemes according to Matsuda, 1965.
Fig. 18.   Diagram to show arrangement of cephalic apodemes in embryo of *Lytta viridana.*
Fig. 19.   Diagram to show tentorium, labral apodemes, antennal apodemes (mandibular ex-
           tensor apodeme), mandibular apodeme (mandibular flexor apodeme), labial apo-
           demes (labial diverticula). 132h embryo of *Lytta viridana.*
Fig. 20.   Diagram to show archicerebrum and segmental cephalic ganglia and important
           cephalic nerves, ventral view.
Fig. 21.   As in Fig. 20, lateral view.
Fig. 22.   A. Annelid-like ancestor of insects to show postoral arrangement of future cephalic
           ganglia. Note prostomium with archicerebrum. B. As above, dorsal view of archi-
           cerebrum and nerve cord.
Fig. 23.   Same as Fig. 22 A, but with cuticle, segmental appendages, and apodemes.
Fig. 24.   A. Hypothetical arthropod in which the first ganglion has shifted into a preoral
           position to form the prosocerebrum, ganglion of the labral segment. B. As above,
           dorsal view of brain and nerve cord.
Fig. 25.   A. Arthropod with primary syncerebrum (Weber)٩= archicerebrum, prosocerebrum,
           deutocerebrum). B. As above, dorsal view.
Fig. 26.   A. Insect head. The tritocerebrum (ganglion of intercalary segment) has moved into
           a preoral position to become part of the brain. The ganglia of the gnathal segments
           fuse to form the suboesophageal ganglion. B. As above, dorsal view.

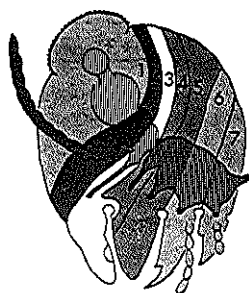# THEORIES OF HEAD SEGMENTATION IN INSECTS

1 Snodgrass, 1960

HEAD OF INSECT
Acron + 4 segments

1- intercalary
2- mandibular
3- maxillary
4- labial

Labrum and Antenna
not appendiculate,
part of acron

2 DuPorte, 1963

HEAD OF INSECT
Acron + 3 segments

1- mandibular
2- maxillary
3- labial

Intercalary absent

3 Butt, 1960

HEAD OF INSECT
Acron + 4 segments

1- intercalary
2- mandibular
3- maxillary
4- labial

Labrum appendiculate,
part of intercalary segment

Antenna not appendiculate, part of acron

4 Ferris, 1950

HEAD OF INSECT
Acron absent,
6 segments

1- labral
2- clypeal
3- oculo-antennal
4- mandibular
5- maxillary
6- labial

intercalary absent

5 Sharov, 1966

HEAD OF INSECT
Acron absent,
7 segments

1- labral
2- preantennal (ocular)
3- antennal
4- intercalary
5- mandibular
6- maxillary
7- labial

6 Roonwal, 1938

HEAD OF INSECT
Acron absent,
7 segments

1- labral
2- preantennal
3- antennal
4- intercalary
5- mandibular
6- maxillary
7- labial

Labrum appendiculate

THEORIES OF HEAD SEGMENTATION IN INSECTS

7   Chaudonneret, 1966

HEAD OF INSECT
Acron small, hidden
7 segments

1- preantennal
2- antennal
3- intercalary
4- superlingual
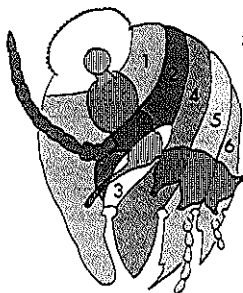5- mandibular
6- maxillary
7- labial

8   Matsuda, 1965
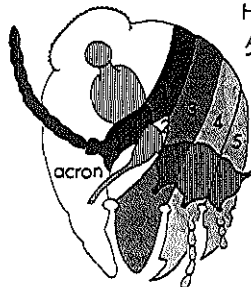
HEAD OF INSECT
Acron large,
5 segments

1- antennal
2- intercalary
3- mandibular
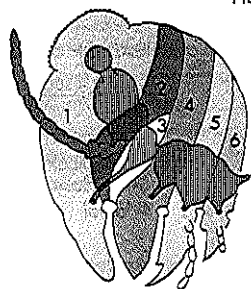4- maxillary
5- labial

9   Imms, 1957; Manton, 1960, 1964

HEAD OF INSECT
Acron + 6 segments

1- preantennal
2- antennal
3- intercalary
4- mandibular
5- maxillary
6- labial

10   Eastham, 1930

HEAD OF INSECT
Acron absent,
6 segments

1- labral
2- antennal
3- intercalary
4- mandibular
5- maxillary
6- labial

Labrum appendiculate,
Premandibular appendages present, vestigial
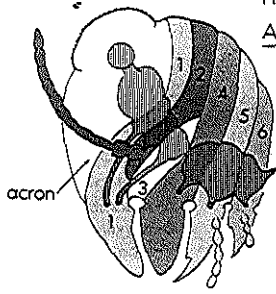
11   Tiegs, 1940, 1947; Weber, 1952
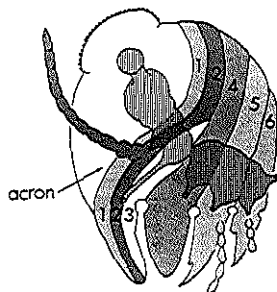
HEAD OF INSECT
Acron + 6 segments

1- preantennal
2- antennal
3- intercalary
4- mandibular
5- maxillary
6- labial

Labrum composite, hence not appendiculate

12   Scholl, 1969; Rempel & Church, 1971
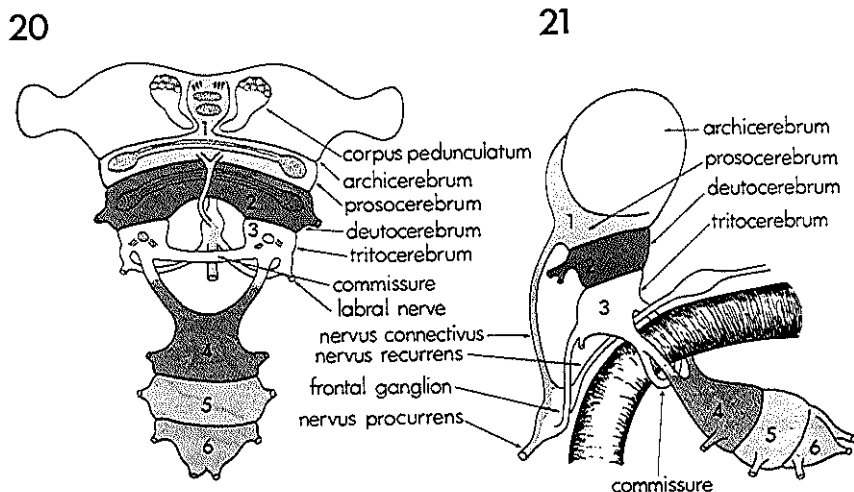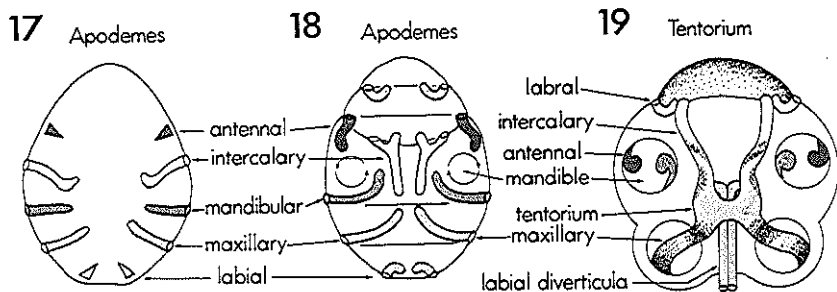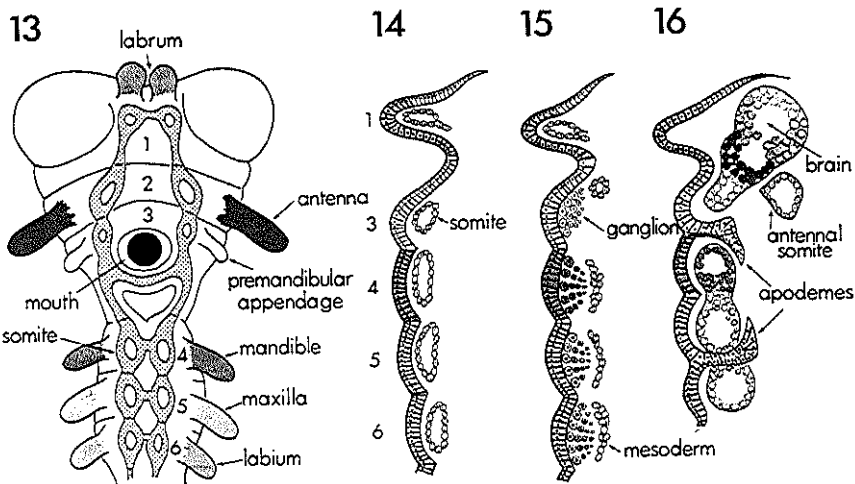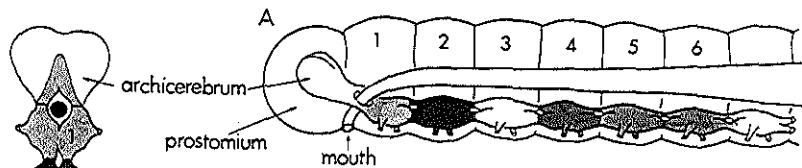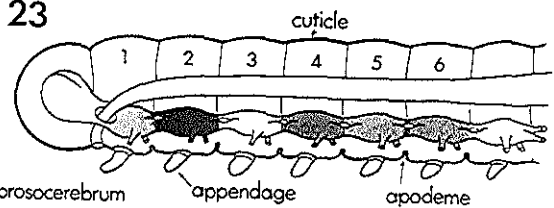
HEAD OF INSECT
Acron + 6 segments

1- labral
2- antennal
3- intercalary
4- mandibular
5- maxillary
6- labial

Labrum appendiculate

13
labrum
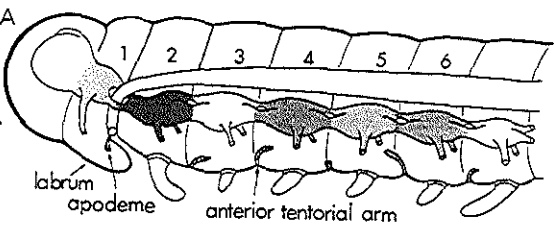1
2
3
antenna
premandibular appendage
mouth
somite
mandible
maxilla
labium

14
1
3 somite
4
5
6

15
ganglion
mesoderm

16
brain
antennal somite
apodemes

17 Apodemes
antennal
intercalary
mandibular
maxillary
labial

18 Apodemes
antennal
intercalary
mandibular
maxillary
labial

19 Tentorium
labral
intercalary
antennal
mandible
tentorium
maxillary
labial diverticula

20
corpus pedunculatum
archicerebrum
prosocerebrum
deutocerebrum
tritocerebrum
commissure
labral nerve
nervus connectivus
nervus recurrens
frontal ganglion
nervus procurrens

21
archicerebrum
prosocerebrum
deutocerebrum
tritocerebrum
commissure

22

archicerebrum

prostomium

mouth

A

cuticle

23

prosocerebrum

appendage   apodeme

A

labrum
apodeme   anterior tentorial arm

24

B

antennal segment

deutocerebrum

B

25   A

antenna

intercalary segment

posterior
tentorial
arm

B

A

tritocerebrum

26

acron
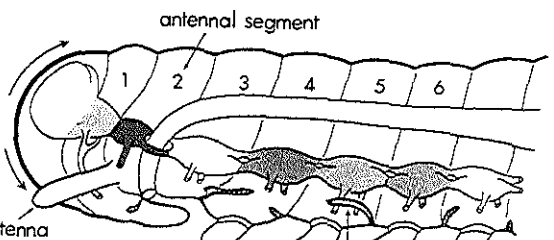
nervus connectivus
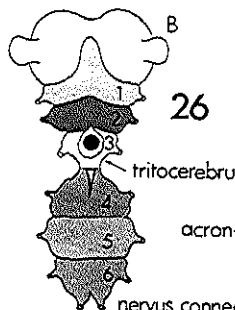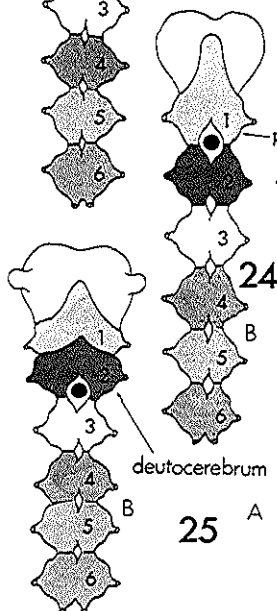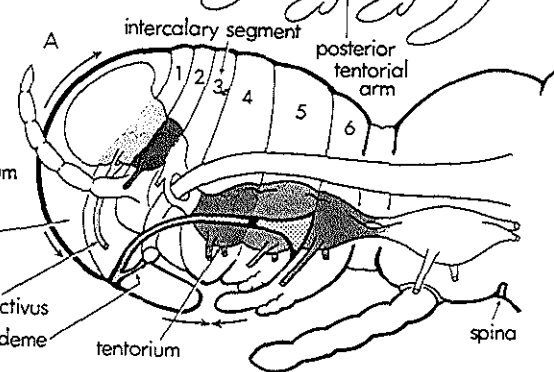
labral apodeme   tentorium

spina

ANTENNAL STRUCTURE AND METAMORPHOSIS IN
FRANKLINIELLA FUSCA (HINDS) (THRIPIDAE) AND
HAPLOTHRIPS VERBASCI (OSBORN) (PHLAEOTHRIPIDAE)
(THYSANOPTERA).

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Larval and adult antennae, in both Frankliniella fusca *and* Haplothrips verbasci, *consist of seven and eight segments respectively. In adults of both species and in larvae of* F. fusca, *the antennae are raised and lowered by levator and depressor muscles inserting into the bases of the scapi and originating on the anterior tentorial arms. Both these muscles, in larvae of* H. verbasci, *have additional branches originating on the vertex of the head.*

Propupal antennae in F. fusca *are short, weakly segmented and forward-directed; those of pupae unsegmented and flexed dorsally over the head and prothorax. During the quiescent stages, both the extrinsic and intrinsic antennal muscles maintain their myofibrils but cease to function because they are no longer attached to cuticle. They increase slightly in diameter and considerably in length, but are unchanged otherwise.*

During the larva II-propupal apolysis of H. verbasci, *all larval head muscles contract maximally; their myofibrils degenerating shortly thereafter. This contraction, plus changes in cell shape probably cause the complete withdrawal of epidermis from within the larva II antennae. At ecdysis, the propupal antennae are evaginated from epidermal pockets as short, unsegmented stubs. In the two pupal stages, they remain unsegmented but lengthen posteriorly along either side of the head. Imaginal segmentation and myofibrils begin to differentiate in the exuvial pharate adult stage.*

Sense organs are similar in type, position, and number in larvae of both species but are very different in adults. No obvious sexual differences exist in the imaginal antennae of either species except for their smaller size in males.

The Johnston's Organ, in larvae of F. fusca, *consists of three chordotonal organs having two scolopidia each; in* H. verbasci *of four having two or three each. In both species, the Johnston's Organ is carried through metamorphosis, two (*H. verbasci*) or three (*F. fusca*) chordotonal organs and additional scolopidia being added to each during the quiescent stages.*

Antennal structure and development in thrips is compared with that occurring in other insects and an hypothesis is offered to explain the origin of the differences in antennal metamorphosis existing between the two species. It is concluded that the drastic events occurring in H. verbasci *and other phlaeothripids have probably evolved in conjunction with the adoption, by this family, of a primarily cryptophilous existence.*

Les antennes de Frankliniella fusca *et de l'*Haplothrips verbasci *aux stades larvaires et adultes consistent respectivement de sept et huit articles. Chez les adultes de chaque espèce et la larve de* F. fusca *les antennes sont elevées et abaissées par les muscles levateurs et dépresseurs. Ces muscles sont attachés à la base des scapes antennaires et sur l'embranchement anterieur du tentorium. Ces deux muscles chez la larve de* H. verbasci *ont des embranchements additionnels allant sur le vertex de la tête.*

Les antennes de la propupe de F. fusca *sont courtes, faiblement articulées et dirigées anterieurement; celles de la pupe ne sont pas articulées et sont orientées dorsalement au-dessus de la tête et du prothorax. Lors des stades inactifs, les muscles intrinsèques et extrinsèques des antennes maintiennent leurs myofibrilles mais cessent toutes fonctions car ils ne sont plus*